Southwest

Great
Plains

Microclimate and Mountain Pine Beetles
in Two Ponderosa Pine Stands in the Black Hills

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Air and bark temperatures, horizontal wind speed, and solar radiation are characterized for ponderosa pine stands considered susceptible and nonsusceptible to attack by the mountain pine beetle in the Black Hills. South-side bark temperatures during midday hours, maximum differences between north-side bark temperatures and air temperatures, maximum differences between south-side bark temperatures and air temperatures, and solar radiation were greater in the nonsusceptible stand than in the susceptible stand. Air temperatures, north-side bark temperatures, and horizontal wind speeds were not significantly different between the two stands. The potential influence of these factors on stand susceptibilty to beetle attack is evaluated.

Keywords: Mountain pine beetle, *Dendroctonus ponderosae*, ponderosa pine, microclimate

Introduction

Infestations of mountain pine beetles (*Dendroctonus ponderosae* Hopkins) may be common in unthinned pine stands but are uncommon in thinned stands. Subtle differences in the biotic and abiotic stand conditions may account for the numbers of beetle-attacked trees in the two types of stands. The abiotic conditions, generally referred to as microclimate, are thought to play an important role.

Epidemics of the mountain pine beetle (MPB) commonly develop in relatively unmanaged stands of pure ponderosa pine (*Pinus ponderosa* Lawson)

according to Sartwell and Stevens (1975). Particularly favorable stands in the Black Hills are usually composed of 75- to 100-year-old, even-aged ponderosa pine with mean stand diameters averaging >8 in dbh and in densities generally exceeding 150 ft² of basal area per acre (Sartwell and Stevens 1975). More recently, stand densities of ≥120 ft² of basal area per acre are considered favorable to epidemics although the extent of the area from which the average basal area is derived may influence what value is considered the critical threshold (Schmid and Mata 1992). For example, stand density in terms of basal area may average 148 ft²/acre for a 2.2-acre plot but the density in 0.1-acre parcels within the 2.2-acre plot may range from 100 ft²/acre to over 200 ft²/acre (Olsen *et al.* 1995).

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In contrast, thinned even-aged ponderosa pine stands with stand diameters averaging ≥10 in dbh and with basal area averaging ≤100 ft²/acre have not sustained substantial MPB-caused mortality (Schmid and Mata 1992) unless some factor creates a primary focus tree within the stand (Eckberg *et al.* 1994). When a primary focus tree was created in a thinned stand with dbh >11 in and basal area equal to 116 ft²/acre, 14 trees were infested (J.M. Schmid 1992, unpublished information). Predisposed trees in thinned stands with similar average diameters and basal areas equal to 60 or 80 ft²/acre resulted in single-tree mortality; but the mortality was not attributable to the MPB nor were MPB-infested spots created around the predisposed tree (J.M. Schmid 1993, unpublished information).

Why MPB epidemics develop in unthinned stands yet fail to develop in thinned stands with similar diameters but lower densities has long been debated. Two hypotheses have emerged to explain MPB success or failure in the two types of stand conditions. One hypothesis attributes the lack of MPB-caused mortality to the function of tree resistance, i.e., the ability of the host to defend itself against MPB attack (Berryman 1978). Tree resistance is reduced in dense, unthinned stands because of competition, old age, or drought; and, therefore, they are susceptible to successful MPB attack (Berryman 1978). In contrast, trees in thinned stands have increased vigor and, therefore, increased resistance because the thinning reduced the competition (Mitchell *et al.* 1983).

The other hypothesis explains the difference in MPB-caused tree mortality in thinned versus unthinned stands on the basis of different microclimates. Thinning increases light intensity, insolation, and temperature (Bartos and Amman 1989). The individual or combined effects of these changes in the microclimate influence MPB attack behavior, deterring or substantially reducing MPB infestation of trees in thinned stands because conditions are unsuitable for attack (Bartos and Amman 1989).

The two hypotheses stress different primary reasons for the lack of MPB infestations in thinned stands. The resistance hypothesis emphasizes the intrinsic physiological condition of the tree as the primary deterrent. The microclimate hypothesis emphasizes the ambient and bark surface physical conditions of the tree as deterring MPB attacks. In essence, beetles attacks are repelled by the tree in the resistance hypothesis, whereas unsuitable ambient and bark surface physical conditions deter beetles from beginning their attacks, according to the microclimate hypothesis.

This note characterizes some microclimatic conditions in a susceptible and a nonsusceptible ponderosa pine stand and evaluates their potential for deterring MPB attack.

Methods

To study the relationship between stand density and MPB-caused tree mortality, a series of growing stock level[2] (GSL) plots were installed in susceptible-size ponderosa pine stands. Between 1985 and 1992, plots were installed in 11 different locations on the Black Hills National Forest in South Dakota. Each series usually consisted of four 2.5-acre plots: three plots cut to GSLs of 60, 80, and 100; or 80, 100, and 120, with the fourth uncut plot serving as a control. The plots were usually cut within one year of installation. Leave trees within cut plots were selected based on diameter, spacing, crown development, and apparent good health. Tree selection emphasized leaving the best, largest trees as evenly spaced as possible.

The White House Gulch plots, located about 10 miles northwest of Custer, SD, were exposed to a natural MPB epidemic (Schmid and Mata 1992). These plots were installed in May 1989 and cut in January 1990. MPB-caused tree mortality in the uncut control plot (GSL 148)[3] has remained about the same from 1989 through 1992 (Schmid and Mata 1992); but the number of attacked trees declined substantially in 1993 as the MPB population decreased sharply (J.M. Schmid 1993, unpublished information). MPB-caused tree mortality has not occurred in the GSL 60 and 80 plots since cutting (Schmid and Mata 1992, J.M. Schmid 1993, unpublished information). Therefore, we consider the White House Gulch GSL 60 and 80 plots as nonsusceptible stands and the uncut control (GSL 148) a susceptible stand.

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[2] *"Growing stock level" is defined as the residual square feet of basal area when average diameter is ≥10 in.*

[3] *Some readers will notice a discrepancy between the GSL value for the White House Gulch control plot in this paper as compared to the value reported in Schmid and Mata (1992). Schmid and Mata erroneously reported the control plot equal to GSL 128 when the correct value was GSL 148. Schmid and Mata apologize for the error.*

After the plots were cut in January 1990, the GSL 80 and uncut control plot (GSL 148) had the following characteristics:

Characteristic	GSL 80	Control
Mean Diameter	11.2"	10.8"
BA per acre	79.2 ft²	148.3 ft²
Tree Spacing	19.3 ft	13.7 ft

To characterize temperature, horizontal wind speed, and solar radiation patterns in the susceptible and nonsusceptible stands, we recorded air and bark temperatures, wind speed, and solar radiation at one location well within the exterior boundaries of each of the uncut control and GSL 80 plots. A central location was chosen in the GSL 80 plot to eliminate possible shading from adjacent stands of greater tree density. At each location, a pipe was driven into the ground to support the housing cabinet which protected the recording equipment.

Bark temperatures at breast height on the north and south sides of five trees in each plot were recorded in degrees Fahrenheit. Temperatures were recorded via YSI (Yellow Springs Instruments) thermilinear thermistor networks[4] attached to cables that were connected to Campbell Scientific 21X microloggers[4]. The thermistor bead portion of each thermilinear thermistor network was placed in a crevice or under a bark scale so it was shaded from direct sunlight. Air temperature was recorded via a YSI thermilinear thermistor network that hung at breast height from the housing cabinet.

The five sample trees were randomly selected from trees surrounding the micrologger. The sample trees in the control plot ranged in diameter from 9.6 to 13.1 in (mean dbh = 11.4 in). Sample trees in the GSL 80 plot ranged in diameter from 9.2 to 12.1 in (mean dbh = 10.5 in). The lower level of live branches on the sample trees and most of the rest of the trees in both plots was at least 15 ft aboveground.

Horizontal wind speed was recorded via a 3-cup anemometer manufactured by Campbell Scientific Inc. One anemometer was attached to the micrologger housing cabinet about 7 ft aboveground in each GSL. The anemometers have a threshold speed of 1 mph and are accurate to ± 0.25 mph.

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[4] The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.

Solar radiation in watts per 10.76 ft² was recorded via a Li-Cor pyranometer[4] that was positioned on the upper surface of the micrologger housing cabinet and about 6 ft aboveground.

Instantaneous air and bark temperatures, wind speed, and solar radiation were recorded every 60 min on the hour during July 21-August 15, 1992. Measurements were made during this period because it coincides with the MPB emergence period (see Schaupp *et al.* 1993). Instantaneous bark temperatures for the north and south sides on the 5 trees were averaged for each hour. Mean bark temperatures for each side were then plotted for their respective hour of each day. Air temperatures were also plotted for each hour of each day for both stands, but each hourly value represents a single instantaneous measurement rather than a mean of five values.

Because MPB generally attack hosts during daylight hours and the greatest number of attacks are initiated after 16:00 (McCambridge 1967), we examined the daily patterns of temperatures, wind speed, and solar radiation for each GSL, and particularly the patterns between 06:00 and 20:00. Air temperatures from each GSL for each hour were subjected to one-way analysis of variance to determine if air temperatures were different between GSLs, a = 0.05. Bark temperatures on the north and south sides of the sample trees in each GSL for each hour were separately subjected to analysis of variance to determine if bark temperatures differed between GSLs on respective aspects, a = 0.05.

Relative differences between air and bark temperatures within each GSL might influence beetle behavior as much or more as differences in bark temperatures between GSLs, so we examined the relationships between air and north-side bark temperatures, and air and south-side bark temperatures in each GSL. We computed the daily maximum difference when the bark temperatures on the north and south sides of each of the five sample trees in each GSL exceeded the respective air temperature. These maximum differences were subjected to analysis of variance to determine if the maximum differences for respective sides were different between GSLs and among days, a = 0.05. We also compared the north-side and south-side bark temperatures of the sample trees in each GSL to their respective air temperatures during each hour of the day in a series of paired t-tests to determine if bark temperatures varied significantly in relation to air temperatures, a = 0.05.

Wind speeds from each GSL were subjected to analysis of variance with hour of day as a repeated measure and days treated as replicates, a = 0.05. Mean instantaneous solar radiation in watts per 10.76 ft² per day was computed for the daylight hours from 06:00 to 20:00. Mean solar radiation at each hour throughout the recording period (July 21-August 15) was also computed for each GSL.

Results and Discussion

Air Temperatures

Air temperatures in the GSL 80 and control plots were not significantly different any hour of the day. Air temperatures in the GSL 80 plot were occasionally 3-4 °F warmer from 1200 to 1700 and frequently 2-5 °F cooler between midnight and 0700 than air temperatures in the control during the same periods (figure 1). Air temperatures in the GSL 80 plot were within ±1.5 °F of those in the control at other times.

Bark Temperatures

Mean north-side bark temperatures in the GSL 80 plot were very similar to mean north-side bark temperatures in the control (GSL 148), differing by a maximum of ±3 °F. Between 10:00 and 16:00, mean temperatures in the GSL 80 plot generally exceeded those in the control by <2 °F on most days (figure 2); but occasionally, mean temperatures in the GSL 80 plot were 2-3 °F warmer. Between 17:00 and 09:00, mean temperatures in the GSL 80 plot differed from those in the control by ≤2 °F; mean temperatures in the control were warmer on some nights.

Mean south-side bark temperatures in the GSL 80 plot were significantly warmer than mean south-side bark temperatures in the control between 12:00 and 18:00 (figure 3). Mean south-side temperatures in the GSL 80 plot were frequently 5-10 °F warmer than the mean south-side temperatures in the control with maximum differences of 10-15 °F between the two GSLs occurring at 12:00 on clear days. On overcast days or partially cloudy days, mean south-side bark temperatures in the GSL 80 plot were only warmer than mean south-side temperatures in the control plot by 2-5 °F between 10:00 and 16:00.

Temperature differences between the mean south-side bark temperatures in the GSL 80 plot and in the control plot ranged from 1-3 °F between 22:00 and 07:00 (figure 3). During most nights, mean temperatures in the GSL 80 plot were 1-3 °F cooler at various hours than mean south-side bark temperatures in the control between 22:00 and 07:00 (figure 3). On the remaining nights, mean south-side bark temperatures in the GSL 80 plot were within ±1 °F of mean south-side bark temperatures in the control plot.
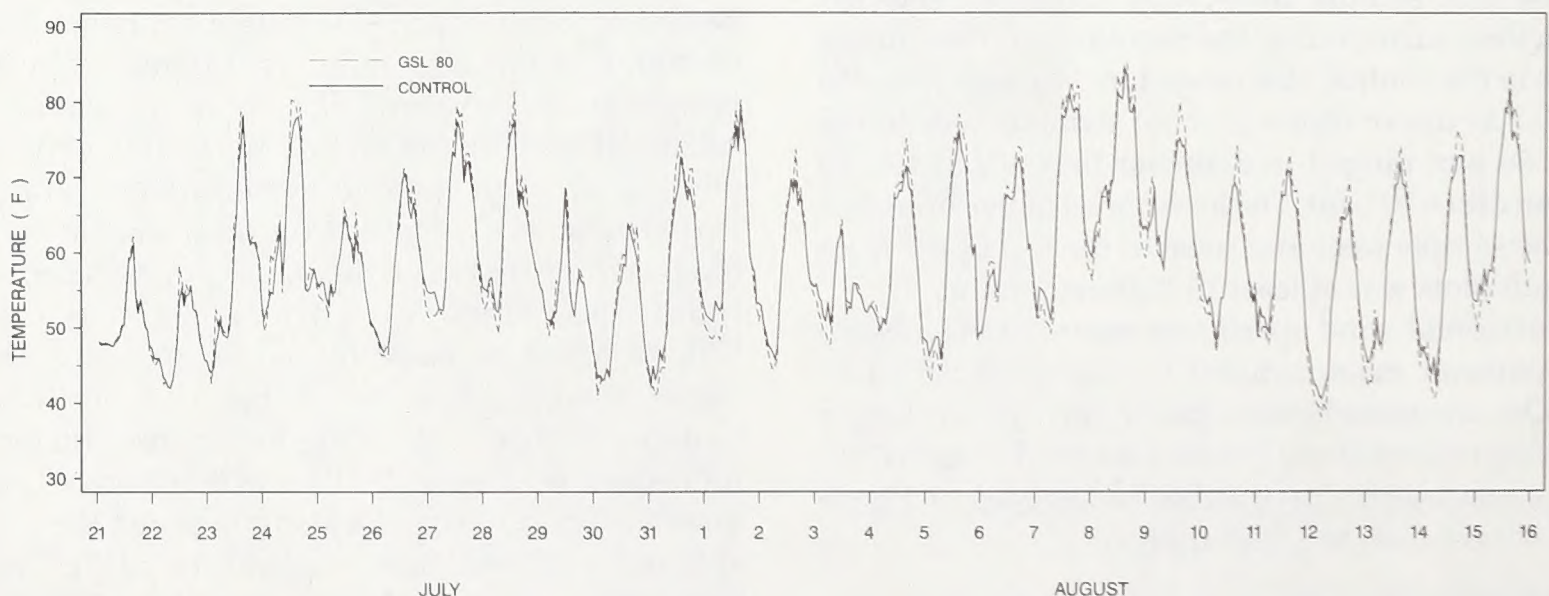

Figure 1.—Air temperatures in degrees Fahrenheit for the GSL 80 and the control (GSL 148). Dashed line represents the GSL 80 and the solid line represents the control.

This pattern of cooler bark temperatures in a GSL 80 stand as compared to an uncut control agrees with patterns observed by Schmid *et al.* (1991). Nocturnal temperatures are influenced by stand density such that lower stand densities allow more thermal reradiation through the canopy and thus lower bark temperatures in the thinned stands (Schmid *et al.* 1991).

The relationship between the mean south-side temperatures in the GSL 80 plot and the control plot varied between 17:00 and 22:00 depending on the conditions during the 6 hours preceeding 17:00. Most of the time, mean south-side temperatures declined from being 3-4 °F warmer than the control to being 0.1-1 °F cooler than the control.

Air-Bark Temperatures

Maximum differences between air and bark temperatures on the north sides of trees in the GSL 80 plot were significantly greater than maximum temperature differences on the north sides of trees in the control plot. The maximum differences between air and bark temperatures were 9 °F for the north sides of trees in the GSL 80 plot and 6 °F for the north sides of trees in the control plot (GSL 148). On a daily basis, approximately 90% of the maximum temperature differences for the north sides in the GSL 80 plot and approximately 80% of the maximum temperature differences for the north sides in the control plot occurred between 19:00 and 06:00.
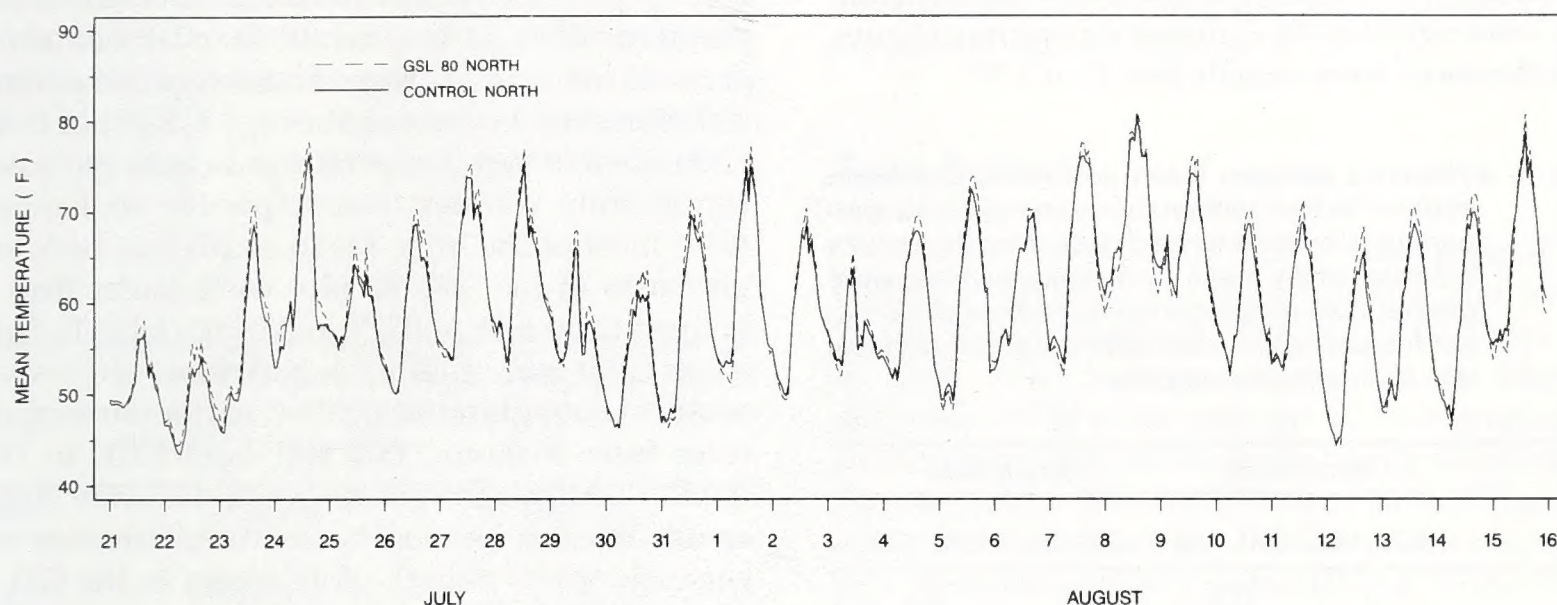

Figure 2.—Mean temperatures in degrees Fahrenheit for the north sides of 5 trees in the GSL 80 and the control (GSL 148). Dashed line represents the GSL 80 and the solid line the control (GSL 148).
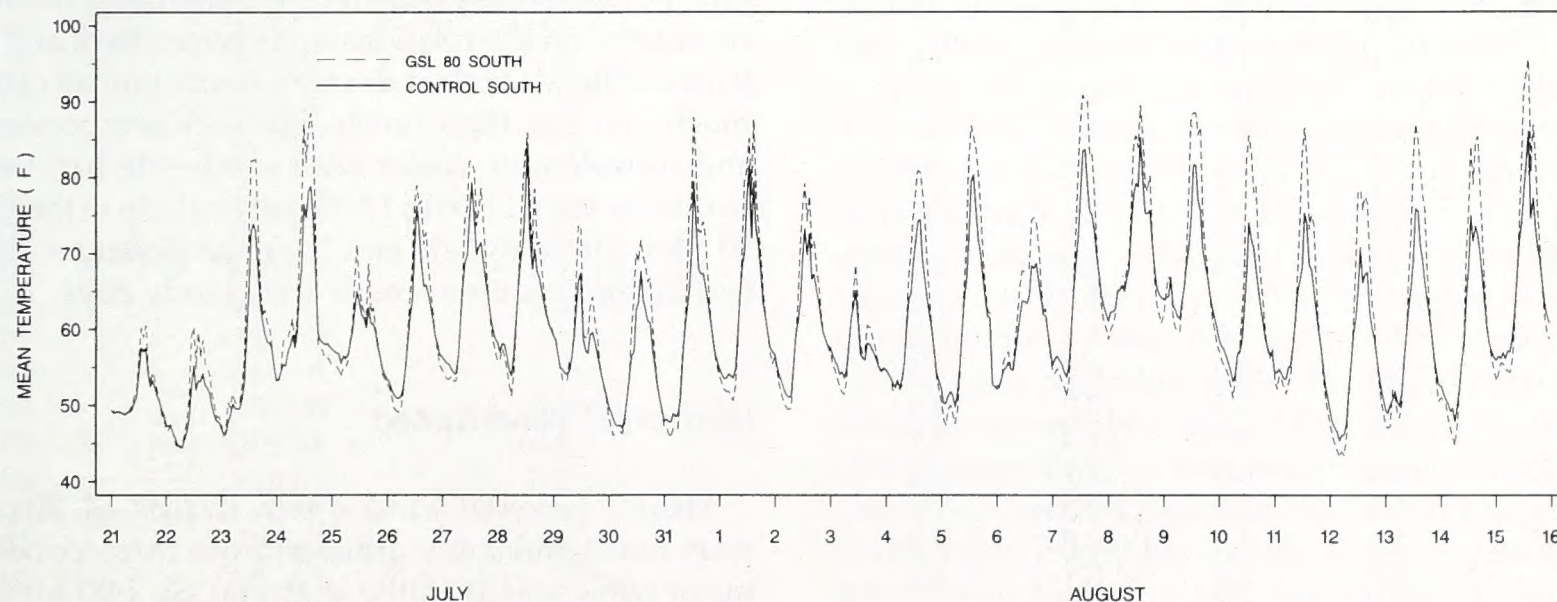

Figure 3.—Mean temperatures in degrees Fahrenheit for the south sides of 5 trees in the GSL 80 and the control (GSL 148). Dashed line represents the GSL 80 and the solid line the control.

The relationship between air and north-side bark temperatures in both GSL plots exhibited similar patterns with respect to the magnitude of differences and to hour of the day; but these patterns varied daily, depending on the weather conditions and GSL. Mean bark temperatures on the north sides of trees in the GSL 80 and control plots were significantly cooler than mean air temperatures between 10:00 and 17:00 (table 1). From 19:00 to 08:00, mean north-side bark temperatures were significantly warmer than air temperatures. At 09:00 and 18:00, differences were either nonsignificant or significantly different in only the GSL 80 plot. The magnitude of differences in both plots was greater during clear days and was less during cloudy or overcast days. Even though the north-side bark and air temperatures were significantly different during most hours, the differences were usually less than 3 °F.

Table 1.—Difference between mean north-side and mean south-side bark temperatures and mean air temperatures by hour for each GSL. Positive values indicate when mean bark temperatures were greater than air temperatures and negative values indicate when mean bark temperatures were less than air temperatures.

Hour	North-side		South-side	
	GSL 80	GSL 148	GSL 80	GSL 148
1:00	2.2	2.4	2.8	2.4
2:00	2.6	1.9	2.2	2.3
3:00	2.2	1.8	1.9	2.2
4:00	2.6	1.8	2.1	2.2
5:00	2.1	1.4	1.8	1.8
6:00	2.2	1.7	1.9	2.1
7:00	2.0	1.6	1.3	1.5
8:00	0.7	0.8	-0.4	-0.3
9:00	-0.3	-0.8	-0.7	-1.0
10:00	-0.8	-1.1	1.4	-0.9
11:00	-2.0	-1.8	3.2	-1.3
12:00	-1.9	-1.5	7.0	0.9
13:00	-1.4	-1.5	6.9	3.3
14:00	-1.5	-0.4	5.8	1.9
15:00	-1.7	-1.3	5.0	0.8
16:00	-0.8	-0.9	4.7	0.1
17:00	-1.0	-0.8	2.9	-0.4
18:00	-0.5	-0.1	1.6	0.1
19:00	0.6	0.3	1.7	0.6
20:00	1.8	1.2	2.3	1.8
21:00	2.6	1.8	2.6	2.3
22:00	2.7	2.2	3.1	2.8
23:00	3.6	2.4	3.3	3.0
24:00	3.7	2.5	3.3	3.0

Maximum temperature differences between air and bark temperatures on the south side of the GSL 80 plot were significantly greater than maximum temperature differences on the south sides of trees in the control plot even though the variances of the maximum temperature differences for the two plots were heterogeneous. Maximum differences between air and south-side bark temperatures were 35 °F for the south sides of trees in the GSL 80 plot and 19°F for the south sides of trees in the control plot. On a daily basis, approximately 90% of the maximum temperature differences for the south sides in the GSL 80 occurred between 11:00 and 17:00 whereas approximately 75% of maximum differences in the control occurred between 06:00 and 18:00. One tree in the control plot nearly always had the maximum temperature difference between 19:00 and 06:00 and thus caused a lower percentage of maximum temperature differences in the control during the daylight hours.

South-side bark temperatures in both plots were significantly warmer than respective air temperatures most of the time. Mean south-side bark temperatures in the GSL 80 plot were cooler than air temperatures only at 08:00 and 09:00 (table 1). In the control plot, mean south-side bark temperatures were cooler or not significantly different from air temperatures from 08:00 to 11:00 and from 16:00 to 18:00 (table 1). Although bark temperatures were significantly different for most hours, the differences were generally ≤3 °F in both plots except in the GSL 80 from 12:00 to 16:00.

Differences between mean bark temperatures for the north and south sides and air temperatures (table 1) do not adequately describe the influence of weather conditions on the relationship between bark and air temperatures. On clear days, air temperatures can be much warmer than north-side bark temperatures and considerably cooler than south-side bark temperatures from 11:00 to 17:00, particularly in the GSL 80 plot. Similarly, air and bark temperatures have less differences on overcast and cloudy days.

Horizontal Wind Speed

Mean horizontal wind speeds in the GSL 80 plot were not significantly different from corresponding mean wind speeds in the control (GSL 148) for any hour of the day (table 2). Wind speeds in the GSL 80 plot were ≤5 mph about 96% of the time, and wind

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speeds in the GSL 148 plot were ≤5 mph about 97% of the time (table 3). Mean wind speeds in both stands were <3.3 mph for any specific hour, and differences between the means were ≤0.6 mph. Although more beetles fly with the wind, especially when wind speeds exceed 5 mph, more beetles will fly against the wind in the presence of attractants when wind speeds are less than 3 mph (Gray *et al.* 1972). Considering the magnitudes of mean wind speeds and their differences, these magnitudes would not substantially influence MPB selection of susceptible versus nonsusceptible stands.

The frequency for specific wind speeds closely follows the frequencies observed by Schmid *et al.* (1992) for comparable GSLs in other sets of plots. Wind speeds >6 mph were recorded ≤2% of the time in two GSL 80 plots (Schmid *et al.* 1992) and were recorded 1.3% of the time in the GSL 80 in this study (table 2). Similarly, wind speeds in an uncut GSL 150 never exceeded 6 mph (Schmid *et al.* 1992); and the

Table 2.—Mean wind speeds (mph) for each hour of the day in the GSL 80 and the GSL 148 plots from July 21 to August 15, 1992. Means are not significantly different for any hour.

Hour	GSL 80	GSL 148
	x ± SD	
01:00	2.1±0.9	2.0±1.0
02:00	2.2±0.9	1.8±1.0
03:00	2.3±0.9	2.0±1.0
04:00	2.4±0.8	2.0±0.9
05:00	2.4±1.0	2.0±1.0
06:00	2.3±1.0	2.2±1.1
07:00	2.1±0.9	1.9±0.9
08:00	2.2±0.9	1.9±1.2
09:00	2.2±1.0	2.4±1.0
10:00	3.1±1.1	2.7±1.1
11:00	3.2±1.2	2.6±1.0
12:00	3.1±1.1	2.6±1.1
13.00	2.8±1.2	2.8±1.3
14:00	3.2±1.2	3.0±1.2
15:00	2.9±0.9	2.6±0.9
16:00	2.8±1.4	2.8±1.5
17:00	2.8±1.5	2.5±1.2
18:00	2.9±1.4	2.6±1.2
19:00	2.0±1.1	1.9±1.0
20:00	1.7±1.0	1.6±0.7
21:00	1.8±1.0	1.7±1.0
22:00	2.0±0.8	1.9±0.8
23:00	2.2±0.8	2.0±0.8
24:00	1.9+0.8	2.0+0.9

Table 3.—Frequency (%) of wind speeds in the GSL 80 and GSL 148 plots.

Wind speed (mph)	GSL 80 (%)	GSL 148 (%)
0-1	14.6	22.8
>1-2	12.8	11.3
>2-3	37.2	36.9
>3-4	24.4	20.0
>4-5	6.9	6.4
>5-6	2.8	2.6
>6-7	0.8	0.0
>7-8	0.5	0.0

same result was observed in our GSL 148 (table 3). And finally, speeds of >2 to 4 mph occurred most frequently in both studies.

Solar Radiation

Solar radiation in the GSL 80 plot generally exceeded solar radiation in the control plot by ≥10 watts/10.76 ft^2 between 07:00 and 19:00. From 11:00 to 15:00, solar radiation in the GSL 80 plot was generally 100 or more watts per 10.76 ft^2 greater than in the control plot with specific hourly differences in the magnitude of 500 to 725 watts/10.76 ft^2 (figure 4). Mean instantaneous solar radiation between 06:00 and 20:00 averaged 175 watts/10.76 ft^2 in the GSL 80 plot and 69 watts/10.76 ft^2 in the control (figure 5). However, mean radiation values for the 14-hour daylight period are misleading because solar radiation at 11:00 to 14:00 was frequently more than 50 times what it was at 07:00 or 20:00 (figure 6).

Although mean solar radiation per day (figure 5) in the GSL 80 plot and the control (GSL 148) generally exhibited similar trends from day to day, on specific days (figure 5, August 2, 8, 14), solar radiation in the control increased, while solar radiation in the GSL 80 plot apparently decreased. We determined in subsequent laboratory tests that water on the sensor lowers the solar radiation value. Because its canopy is much more open than that of the control, the GSL 80 plot is more likely to have water on the sensor after rain. Thus, solar radiation in the control was greater than in the GSL 80 for specific hours (figure 4) and mean solar radiation per day exhibited opposite trends (figure 5). Further, the water effect obviously lowered radiation values for specific hours on cer-
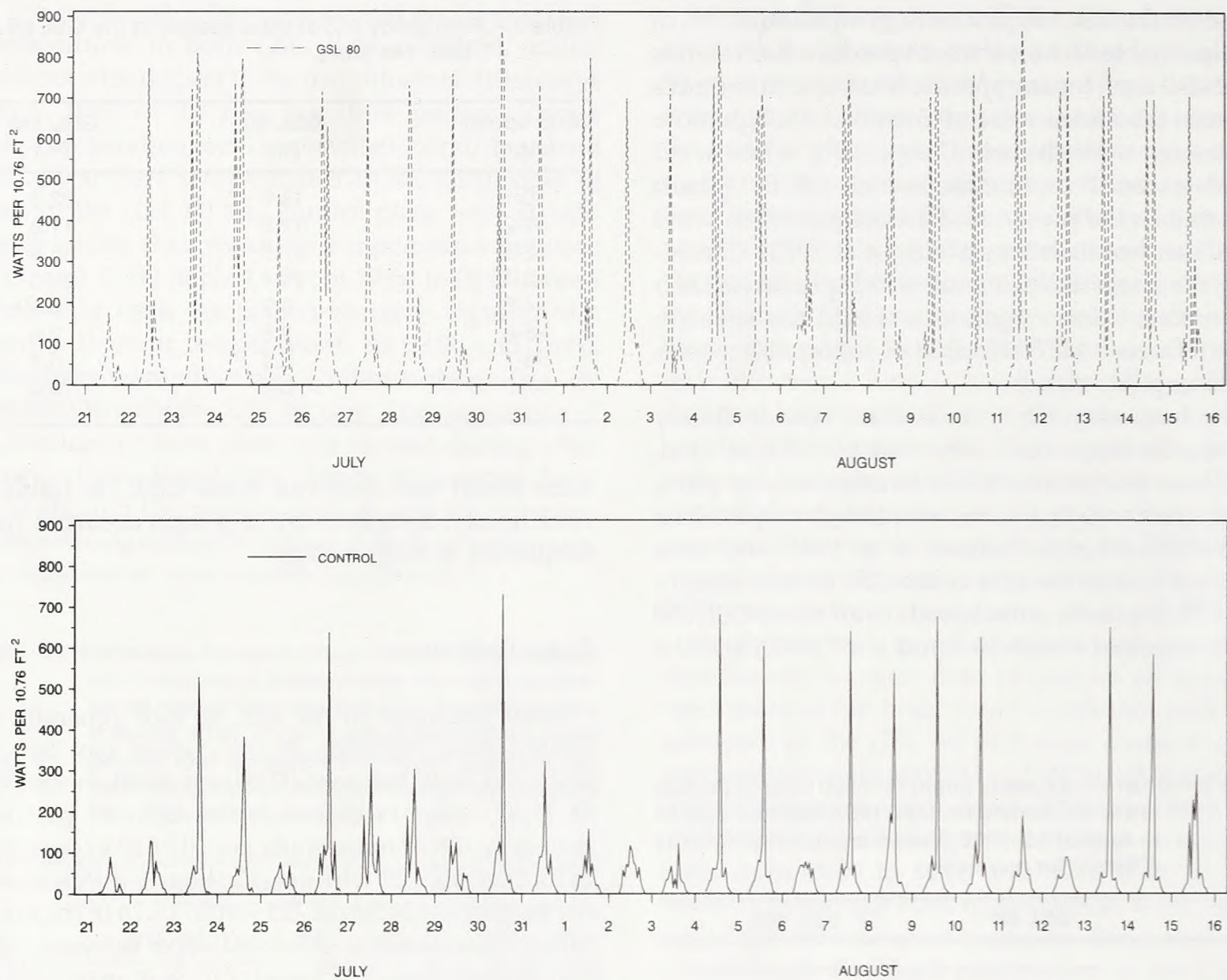
Figure 4.—Solar radiation (watts per 10.76 ft²) for the GSL 80 (top) and the control (bottom) from July 21 to August 15, 1992.
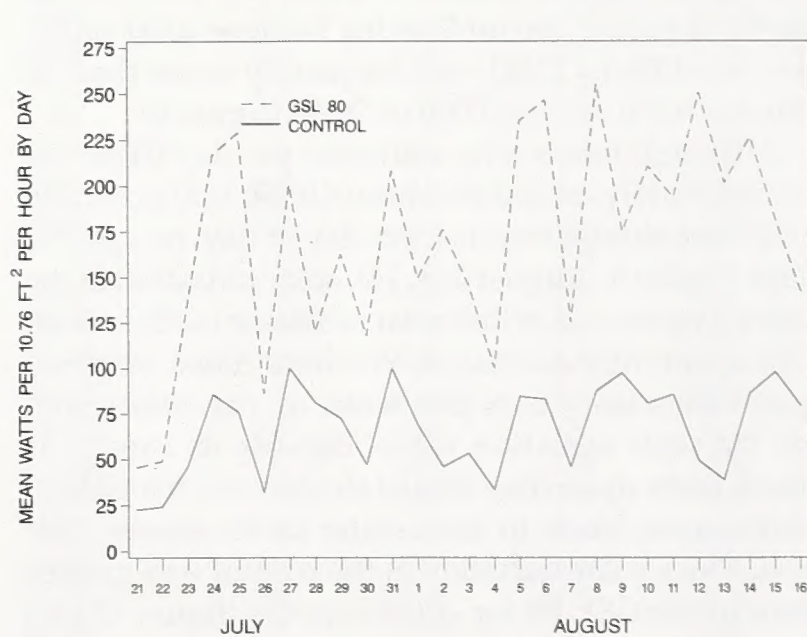

Figure 5.—Mean solar radiation (watts per 10.76 ft²) per day from 06:00 to 20:00 for the GSL 80 and the GSL 148 from July 21 to August 15, 1992.
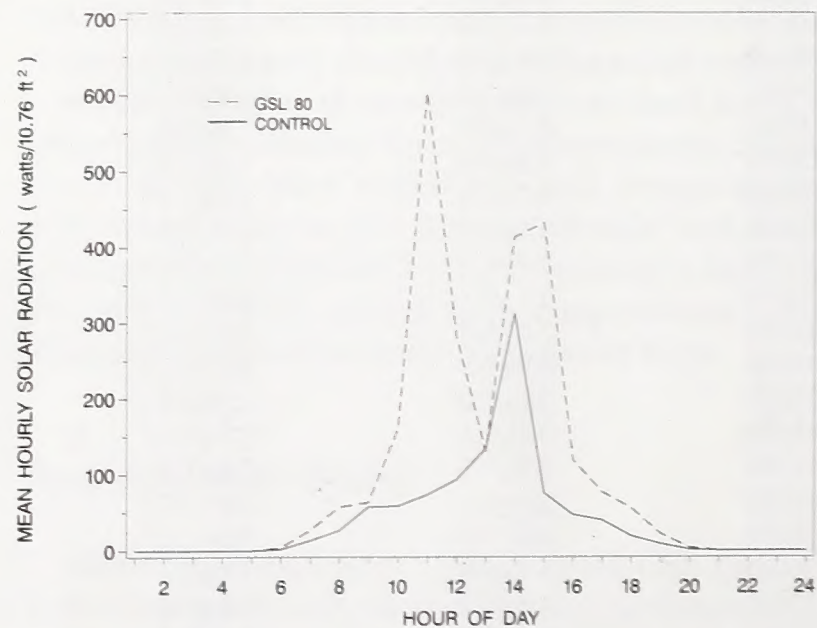

Figure 6.—Mean solar radiation (watts per 10.76 ft²) per hour for the GSL 80 and the GSL 148 from July 21 to August 15, 1992.

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tain days and thus lowered mean values. We believe this effect was short-lived in most instances because the water evaporated when skies cleared after the storm passed. In those instances when the water might have remained on the sensor for several hours because of prolonged overcast skies, the water effect on radiation values was probably considerably less than the influence of overcast skies.

Mean solar radiation per hour (figure 6) best depicts the differences between the two stocking levels and the influence of weather and stand density on solar radiation beneath the canopy. Solar radiation differences between the two stands increased substantially betwen 09:00 and 10:00 on clear days. Maximum differences occurred between 11:00 and 15:00 with differences decreasing rapidly after 15:00. From 11:00 to 15:00, solar radiation in the GSL 80 plot would have probably exceeded solar radiation in the control by 300 to 450 watts on clear days but the formation of clouds around 12:00 and frequent rain between 11:00 and 14:00 altered this pattern. Generally, solar radiation under the canopy in the control did not exceed 150 watts during the day except at 14:00, when an opening in the canopy permitted solar radiation directly on the sensor.

Characteristics of a Susceptible Stand

The susceptible stand (GSL 148) was characterized by the following conditions during the MPB emergence period: (1) air temperature at breast height never exceeded 86 °F and rarely exceeded 80 °F; (2) mean north-side bark temperatures never exceeded 81 °F and rarely exceeded 77°F; (3) mean south-side bark temperatures never exceeded 86 °F and rarely exceeded 80 °F; (4) maximum differences between north-side bark temperatures and air temperatures were ≤ 6 °F and occurred during nighttime hours; (5) mean north-side bark temperatures were usually less than air temperatures between 10:00 and 17:00; (6) maximum differences between south-side bark temperatures and air temperatures were ≤ 19 °F and occurred in the afternoon; (7) mean south-side bark temperatures were usually greater than air temperatures but the difference was ≤ 3°F; (8) horizontal wind speeds never exceeded 6 mph and 90% of the time were <4 mph; (9) mean instantaneous solar radiation beneath the canopy rarely exceeded 150

watts per 10.76 ft^2 between 06:00 and 20:00 except directly under openings where instantaneous measurements reached 600 to 730 watts/ 10.76 ft^2.

Characteristics of a Nonsusceptible Stand

The nonsusceptible GSL 80 stand was characterized by the following conditions during the MPB emergence period: (1) air temperature at bh never exceeded 85 °F and rarely exceeded 80°F; (2) mean north-side bark temperatures never exceeded 81 °F and rarely exceeded 77°F; (3) mean south-side bark temperatures never exceeded 96 °F but frequently exceeded 80°F between 1200 and 1500; (4) maximum differences between north-side bark temperatures and air temperatures were ≤ 9 °F and occurred during nighttime hours; (5) mean north-side bark temperatures were usually less than air temperatures between 10:00 and 18:00; (6) maximum differences between south-side bark temperatures and air temperatures exceeded 19 °F about 24% of the time and occurred in the afternoon; (7) mean south-side bark temperatures were nearly always greater than air temperatures and averaged ≥ 5 °F warmer from 12:00 to 16:00; (8) horizontal wind speeds exceeded 6 mph <1% of the time and were <4 mph 89% of the time; (9) mean instantaneous solar radiation beneath the canopy generally exceeded 150 watts/10.76 ft^2 between 10:00 and 15:00 and frequently exceeded 300 watts/10.76 ft^2 for several hours.

Stand Microclimate and MPB Infestation

Of the microclimatic variables evaluated, south-side bark temperatures, maximum differences between south-side bark temperatures and air temperatures, differences between mean south-side bark temperatures and air temperatures, and solar radiation were substantially different enough between the nonsusceptible stand (GSL 80) and the susceptible stand (GSL 148) to influence the infestation of their respective stands.

The warmer south-side temperature conditions in the GSL 80 stand might be enough to discourage MPB from initiating attacks. When south-side temperatures exceed 89 °F, as they did occasionally between 11:00 and 14:00, such temperatures are above the optimum range for beetle flight (Safranyik 1978).

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During these hours when south-side bark temperatures exceed the optimum conditions and the south-side bark temperatures may be more than 20 °F warmer than air temperatures, the combined temperature conditions may be severe enough to deter attacks on the south side (see Shepherd 1966). However, south-side temperatures were usually below 85 °F after 15:00 and were within the optimum temperature range for MPB activity (Safranyik 1978) for several hours thereafter. And the differences between south-side bark temperatures and air temperatures substantially subside after 17:00 even though they may remain significantly different. Because most MPB attacks are initiated in late afternoon (McCambridge 1967), MPB attacks could readily commence on south sides during these hours. Thus, although "hot south-side bark temperatures" may deter MPB attacks between 11:00 and 14:00 (Bartos and Amman 1989), temperatures on the south sides would be more conducive to, rather than a deterrent for, attacks during late afternoon and early evening.

Temperature conditions on the south sides of trees may be important, but the argument ignores the role of the north-side temperature conditions. North-side temperatures on trees in the GSL 80 stand were generally less than 2 °F warmer than north-side temperatures in the susceptible stand and were within the optimum temperature range for MPB activity (Safranyik 1978) during the day. Further, although maximum differences between north-side bark temperatures and air temperatures were significantly different between the two plots, the relationship between mean north-side bark temperatures and air temperatures (table 1) was almost identical in both plots. Therefore, it seems unlikely that north-side temperatures would discourage MPB from initiating attacks on the north side of trees in either plot during any time of the day—a conclusion consistent with the observations of Bartos and Amman (1989) on lodgepole pine (*P. contorta* Douglas). If attacks begin on the north sides, then those attacks would attract additional MPB, which would eventually spread to the south side and begin attacks thereon when high south-side temperatures moderated in late afternoon.

Solar radiation was obviously different between the two stands but how it would affect host selection is unclear. High intensity light stimulated flight and attracted MPB beetles (Shepherd 1966). These observations might suggest that MPB would be attracted to stands with higher light intensities i.e., the GSL 80

stand. However, extrapolating Shepherd's observations on MPB response to light intensities to explain stand selection is improper because his observations concerned the influence of light on the initiation of flight and not its influence once the beetles attained flight. Further, MPB infestations in GSL 80 stands are rarely observed so this conclusion would not follow. Shepherd (1966) also noted that the beetles' tendency to move toward higher light intensities must be neutralized or reversed after initial dispersal for beetles to attack the lower part of the tree. Thus, MPB may have a negative phototactic response to high light intensities after initial flight which would cause them to avoid stands (i.e., GSL 80) with such light characteristics.

We did not record vertical air movement in this study, so we cannot state whether it was different between the two stands. A previous study indicated no significant difference in vertical wind speeds between thinned stands and their uncut controls (Schmid et al. 1992). However, convection currents— below the sensitivity of our wind speed measuring devices in that study—may influence pheromone movement (Schmid et al. 1992). These currents could disrupt pheromone movement (Bartos and Amman 1989) and, therefore, the beetle's ability to locate susceptible trees.

Considering the potential effects of the different microclimatic variables we evaluated and others investigated in previous studies, only solar radiation and, perhaps, vertical air movement or turbulence would appear to play an important role in MPB selection of particular stands. The influence of solar radiation is generally unknown and needs more work. Because vertical air movement also tends to subside in late afternoon, even its role seems less important than tree susceptibility. Although the cumulative effect of all the microclimatic factors may play a role in MPB stand selection, our general feeling is that microclimate indirectly influences MPB stand selection behavior through its influence on the behavior and dispersion of attractant chemicals rather than its direct influence on beetle behavior. Some will argue that catches of relatively equal numbers of MPB in thinned and unthinned stands (Schmitz et al. 1980, Bartos and Amman 1989) coupled with greater numbers of infested trees in unthinned stands versus thinned stands are prime evidence for the influence of microclimate (G.D. Amman 1993, personal communication). Indeed it might be, but the lack of

infested trees in thinned stands in the presence of large numbers of beetles is not conclusive evidence that microclimate discouraged the beetles. The conclusion could also be drawn that the beetles failed to find susceptible trees in the thinned stands and flew elsewhere.

The minimal infestation of thinned ponderosa pine stands by the MPB may not be primarily influenced by either intrinsic host resistance or microclimate to the extent currently envisioned. If predisposition influences MPB selection of ponderosa pine as Eckberg et al. (1994) propose, MPB may not infest leave trees in thinned stands for 10 to 20 years after harvesting because nearly all the most susceptible trees—the potential primary focus trees—would have been removed during harvesting. By selecting the best trees as leave trees, cutting would generally remove the predisposed trees—those trees with inferior crowns, diseases, physical damage (lightning-struck), or evidence of scolytid activity including prior MPB attacks, which the beetle would be inclined to select. However, a few susceptible trees may be present in thinned stands, especially stands with basal areas of >80 ft^2/acre, despite prudent leave tree selection. These trees may or may not be attacked because vertical air movement disrupts the source of attraction from the susceptible tree(s) and makes it difficult for attacking beetles to locate them.

Some readers will interpret our conclusions as support for the resistance hypothesis because of our frequent usage of susceptibility in this manuscript and their interchangeable usage of susceptibility and resistance (see Coulson et al. 1985). Most forest entomologists commonly interchange susceptibility and resistance because susceptibility is thought to increase as resistance decreases and vice versa (Berryman 1982) such that the relationship between the two terms could be described by the equation S (susceptibility) = 1 - R (resistance) or S = 1/R. The relationship may be that straightforward if resistance strongly influences susceptibility. However, Barbosa and Wagner (1989) define susceptibility as the probability of beetle attack (MPB attack in our case) and Berryman (1978) defines resistance as the ability of a host tree to defend itself against MPB attack. Susceptiblity and resistance are thus only related because the conditions (drought, diseases, etc.) usually ascribed to increasing susceptibility are also ascribed to lowering resistance. We are not yet convinced of the tight affinity of the two terms be- cause we are not sure resistance, as currently defined, strongly influences susceptibility to the degree generally accepted.

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